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Far-Red Reversal of Red Light Effect during Long-Night Induction of Potato (*Solanum tuberosum* L.) Tuberization[1]

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ABSTRACT

The hypothesis that phytochrome is involved in the regulation of potato (*Solanum tuberosum* L.) tuberization was tested. When 5 minutes of red light were given in the middle of the 16-hour dark period to which whole plants were exposed daily for 14 days before making cuttings, the percentage of tuberization on cuttings decreased. The effect of red light was significantly reversed by 2 minutes of far-red light given immediately after the red in each of two separate experiments. This supports the hypothesis that phytochrome is at least indirectly involved.

Longer exposures to red light were not always as effective as a 5-minute exposure in reducing tuberization and were not reversible by far-red light.

It has been assumed that potato tuberization is under the control of phytochrome because phytochrome has been implicated in many photoperiodic reactions, and tuberization in potatoes is affected by photoperiod. Garner and Allard (6) and many others have shown that tuberization is enhanced by short days, although short days do not always increase yield because maturity is also hastened (13). Some species of potato require short days before tuberization can occur. Rasumov (11) reported that *Solanum demissum* is in this category. He also reported that long days substantially delayed tuberization of *S. tuberosum* ssp. *andigena*. Other species that tuberize under short days include Jerusalem artichoke (*Helianthus tuberosus*), *Begonia evansiana*, Scarlet runner bean (*Phaseolus coccinius*), and several species of Dahlias. Of these, only *B. evansiana* has been investigated in regard to phytochrome involvement in its tuberization response, and was shown by Esashi (3) to be controlled by phytochrome. Koukkare and Hillman (7) found a high level of phytochrome in the tips of potato tuber sprouts, which strongly suggests that potato leaves contain phytochrome.

Another reason that phytochrome involvement in potato tuberization has been generally assumed is that tuberization is delayed, reduced, or eliminated if light is shone on the plants during the long nights that would normally induce tuberization. Twenty min of white light in the middle of long nights delayed tuber initiation and reduced tuber number and weight in *S. tuberosum* and *S. demissum* (10). Slater (12) reported that a light break in the middle of the night delayed tuberization in *S. tuberosum* cv. 'Arran Pilot' and stopped tuber initiation completely in *S. demissum*. MacDonald (9) found that 5 min of R[2] in the middle of a 16-h dark period was effective in reducing tuber number per plant on *S. tuberosum* cv. 'Up-to-Date.' She tried to reverse the R effect with FR but was unsuccessful. She speculated that this was due to a short delay, necessitated by her illumination system, between the cessation of the R and the commencement of the FR.

We report here the FR reversal of the R effect, confirming a role of phytochrome in potato tuberization.

MATERIALS AND METHODS

S. tuberosum ssp. *andigena* was used instead of *S. tuberosum* for this research to get a more qualitative difference in tuberization between inducing and noninducing treatments. Two clones were obtained by making selections from seeds derived from No. 512 of the Wageningen Potato Collection. The original introduction was from Peru. There was segregation for response to photoperiod, but clones were selected that required short days for tuberization. Plants were found to be free from potato virus Y using the host plant (*S. demissum*) diagnostic technique.

Stock plants of each clone were propagated by cuttings and grown in a peat-vermiculite mix (1) in 26.6-L nursery pots. They were fertilized once a week. The greenhouse was set for 20°C day and 16°C night temperatures. In the spring, fall, and winter, natural light was supplemented by metal halide lamps (Sylvania 1000-w 'Metalarc'). These were spaced 1.2 m apart and were 3 m above bench level. PAR at plant level ranged from 270 to 285 μE m^{-2} s^{-1}. In the spring, fall, and winter, the halide lamps were left on continuously. The daylength during the summer was extended to 24 h using 100-w incandescent lamps 1.5 m above bench level. These provided 2.5 μE m^{-2} s^{-1} of PAR (110 lux). The stock plants were pinched back to produce many lateral shoots, and they were left unstaked so that every shoot was approximately the same distance away from the lamps, owing to the sprawling habit of the plants.

When a suitable number of shoots was produced, apical cuttings 15-cm long were taken from the shoots. The cuttings were placed in a mist bench equipped with incandescent lamps that were set to extend the photoperiod to 24 h. After the cuttings were rooted, they were removed from the mist bench and fertilized. They were allowed to recover in the greenhouse for 4 to 5 d before being put in the growth chambers. Fertilizer was withheld during the treatment period.

The growth chambers used were Sherer, Model 63–10. The temperature was set at 20°C during dull light and 16°C during darkness or periods of dim light. The daylength was 8 h of full light. When a 16-h day was one of the treatments, 8 h of dim incandescent light (2.8 μE m^{-2} s^{-1} of PAR) were added to the 8-h day to extend the photoperiod. The growth chambers provided about 275 μE m^{-2} s^{-1} of PAR at plant height.

Three growth chambers were fitted with four additional 81.3-cm Sylvania 'cool white' color fluorescent lamps mounted at the top of the front and back sides of the chambers about 70 cm above plant level. These lamps were used for the R source. They were

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[2] Abbreviations: R, red light; FR, far-red light.

covered with four layers of red cellophane (from Nasco Agricultural Sciences). The irradiance at plant level was 0.13 μw cm^{-2} nm^{-1} at 660 nm as measured by a calibrated ISCO SR spectroradiometer. The FR source was two 300-w incandescent flood lamps mounted 5 cm apart. A 10-cm water barrier in front of the lamps eliminated burning of the plants from IR radiation. The light from the fixture was filtered by two layers of blue and three layers of red cellophane to obtain the FR. The blue cellophane was also obtained from Nasco. The irradiance at plant level was 9.0 μw cm^{-2} nm^{-1} at 735 nm.

The intense R source was eight 1.2-m Sylvania 'daylight' color fluorescent lamps spaced 2 cm apart. These lamps were covered with four layers of red cellophane and were suspended 12 cm from the top of the plants. The irradiance at plant level was 4.8 μw cm^{-2} nm^{-1} at 660 nm.

Light treatments were given in the middle of the dark period and continued for 14 cycles. Then one apical cutting and two single-node (leaf + axillary bud) cuttings were taken from each plant. The two types of cuttings (4, 5) were taken to increase the number of cuttings that could be obtained from each plant. As found previously (5), the two types gave similar results; and data from both types were pooled for analysis of variance. Cuttings were used, instead of observing tuberization on the whole plants, because cuttings provide a convenient, accurate determination of the extent of induction (5). The cuttings were placed in a mist bench provided with lights that extended the photoperiod to 24 h. After 2 weeks, the underground bud at the base of each cutting was examined and the type of growth there (tuber, stolon, leafy shoot, or dormant bud—see Ref. 4 for illustrations) was recorded.

Percentages of tuberization values were transformed using the arcsin transformation before statistical analysis was performed. Mean separation by Duncan's multiple range test was used on all data. In no experiment was there a statistically significant effect due to replications or clones.

RESULTS

Night Interruption with R. Preliminary experiments showed that 15 min of R in the middle of the dark period had no inhibitory effect on tuberization. This time period was chosen because previous researchers used it routinely in these chambers to affect the growth habit of beans (8). Longer periods of exposure to R were tested next. In the first experiment, 30 min of R reduced tuberization significantly, but 45- or 60-min exposures were much more effective (Table I). Experiments 2 and 3 showed that 75 s (Table I) or 2 min (Table II) of intense R also decreased tuberization.

In a treatment similar to one used with *Chrysanthemum* (2), potato plants were exposed to three 5-min periods of R spaced 1 h apart, in the middle of the dark period. This eliminated all tuberization (Table III, experiment 5). In a follow-up experiment, three 5-min periods of R, two 5-min periods of R, and one 5-min period of R were used. Three and two periods of R eliminated tuberization; and, although preliminary experiments had shown that 15 min of R had no effect on tuberization, 5 min of R reduced tuberization significantly (Table III, experiment 6).

The efficacy of 5 min R compared to longer exposures was verified in experiment 7 (Table IV), where 45 min R inhibited tuberization significantly less than did 5 min R.

Reversal of R effects by FR. Several attempts to reverse the effects of R by FR were unsuccessful. Dosages of 38-min and 60-min R were found to be irreversible by subsequent exposure to 2 min, 30 s and 3 min 20 s, respectively, of FR (Table II, experiments 3 and 4). Effects of 2 min of intense R were not ameliorated by 6 min of FR (Table II, experiment 3).

However, 5-min treatments with R were reversed by FR in two separate experiments (Table V). In experiment 8, 16-h nights gave 47% tuberization compared to none on cuttings taken from plants that received 8-h nights. Interruption of the dark period with 5-min R almost eliminated tuberization, and 2 min of FR immediately after the R significantly restored it, although not to the level of tuberization obtained from long nights.

Experiment 9, a repetition of experiment 8, contained an extra treatment that tested the effects of 2-min FR alone. Tuber induction was stronger from the 16-h night than it was in experiment 8, but the basic results were confirmed (Table V). In experiment 9, FR alone had a significant inhibitory effect on tuberization. This was expected, because the FR light source emitted a small proportion of light in the red region.

In addition to increasing tuberization of underground buds on cuttings, exposure of potato plants to short photoperiods increases the tendency of nontuberizing buds to grow as leafy shoots or stolons rather than remaining dormant (5). It was clear from our results that R in the middle of long nights increased bud dormancy on cuttings (data not shown). FR reversal of this effect was not consistent and will require further investigation.

Table I. *Tuberization on Cuttings from Plants Given Various R Exposures, Experiments 1 and 2*

Light treatments were given in the middle of the dark period and were continued for 2 weeks before cuttings were taken. Cuttings were inserted into potting medium and maintained in a mist bench under continuous illumination for 2 weeks. There were four replications in each experiment.

Light Treatment	Tuberization on Cuttings	
	No. of cuttings observed	Percentage tuberized[a]
Experiment 1		
16-h Night	94	84 a
30-min R	66	50 b
45-min R	63	2 c
60-min R	65	0 c
Experiment 2		
16-h Night	43	98 a
75-s intense R	56	16 b

[a] Within an experiment, percentages followed by the same letter (a, b, c) are not different at the 5% level using Duncan's multiple range test.

Table II. *Unsuccessful Attempts to Reverse Effects of R with FR, Experiments 3 and 4*

FR was given immediately after the R. Other details were as described in Table I.

Light Treatment	Tuberization on Cuttings	
	No. of cuttings observed	Percentage tuberized[a]
Experiment 3		
16-h Night	52	64 a
2-min intense R	52	14 b
2-min intense R + 6-min FR	64	16 b
38-min R	51	0 c
38-min R + 2-min, 30-s FR	59	21 c
Experiment 4		
16-h Night	94	52 a
60-min R	89	0 b
60-min R + 3-min, 20-s FR	92	0 b

[a] Within an experiment, percentages followed by the same letter (a, b, c) are not different at the 5% level using Duncan's multiple range test.

DISCUSSION

Confirming the observations of MacDonald (9), exposure of potato plants to R in the middle of long nights had an inhibitory

Table III. *Effects of Repeated Short Exposures to R, Experiments 5 and 6*

See description in Table I for details of the experiments.

Light Treatment	Tuberization on Cuttings	
	No. of cuttings observed	Percentage tuberized[a]
Experiment 5		
16-h Night	68	47 a
Three 5-min periods of R, 1 h apart	82	0 b
Experiment 6		
16-h Night	38	50 a
5-min R	48	19 b
Two 5-min periods of R, 1 h apart	32	0 c
Three 5-min periods of R, 1 h apart	48	0 c

[a] Within an experiment, percentages followed by the same letter (a, b, c) are not different at the 5% level using Duncan's multiple range test.

Table IV. *Effects of Various R Exposures on Tuberization, Experiment 7*

There were eight replications. Other details were as described in Table I.

Light Treatment	Tuberization on Cuttings	
	No. of cuttings observed	Percentage tuberized[a]
Experiment 7		
16-h Night, control	106	45 a
5-min R	93	2 c
30-min R	101	0 c
45-min R	110	11 b

[a] Percentages followed by the same letter (a, b, c) are not different at the 5% level using Duncan's multiple range test.

effect on tuberization. This effect is similar to that obtained by shortening the dark period. Increasing the length of the R exposure did not always produce a corresponding degree of increased effectiveness. The optimal R exposure time seemed to vary somewhat from one experiment to the next, but in one case 5 min was significantly more effective than 45 min (Table IV).

There appeared to be a reaction to large dosages of R that was not reversible by FR. This was observed after 30 min or more of R, or after 2 min of high intensity R. However, the reduction in the tuberization produced by 5-min R was reversed by FR both times it was attempted.

We conclude that phytochrome is involved directly or indirectly with regulation of potato tuberization.

Table V. *Reversal of R Effects by FR, Experiments 8 and 9*

Control treatments consisting of 16- and 8-h nights were also included. FR was given immediately after the R in the R + FR treatment. There were eight replications. Other details were as described in Table I.

Light Treatment	Tuberization on Cuttings	
	No. of cuttings observed	Percentage tuberized[a]
Experiment 8		
16-h Night	137	47 a
5-min R	133	3 c
5-min R + 2-min FR	144	26 b
8-h Night	135	0 c
Experiment 9		
16-h Night	132	81 a
5-min R	116	30 d
5-min R + 2-min FR	120	55 c
2-min FR	121	69 b
8-h Night	121	0 e

[a] Within an experiment, percentages followed by the same letter are not different at the 5% level using Duncan's multiple range test.

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